

## FOREST FLOOR DEPTH MEDIATES UNDERSTORY VIGOR IN XERIC *PINUS PALUSTRIS* ECOSYSTEMS

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**Abstract.** Longleaf pine (*Pinus palustris*) woodlands and savannas are among the most frequently burned ecosystems in the world with fire return intervals of 1–10 years. This fire regime has maintained high levels of biodiversity in terms of both species richness and endemism. Land use changes have reduced the area of this ecosystem by >95%, and inadequate fire frequencies threaten many of the remnants today. In the absence of frequent fire, rapid colonization of hardwoods and shrubs occurs, and a broad-leaved midstory develops. This midstory encroachment has been the focus of much research and management concern, largely based on the assumption that the midstory reduces understory plant diversity through direction competition via light interception. The general application of this mechanism of degradation is questionable, however, because midstory density, leaf area, and hardwood species composition vary substantially along a soil moisture gradient from mesic to extremely xeric sites. Reanalysis of recently reported data from xeric longleaf pine communities suggests that the development of the forest floor, a less conspicuous change in forest structure, might cause a decline in plant biodiversity when forests remain unburned. We report here a test of the interactions among fire, litter accumulation, forest floor development, and midstory canopy density on understory plant diversity. Structural equation modeling showed that within xeric sites, forest floor development was the primary factor explaining decreased biodiversity. The only effects of midstory development on biodiversity were those mediated through forest floor development. Boundary line analysis of functional guilds of understory plants showed sensitivity to even minor development of the forest floor in the absence of fire. These results challenge the prevailing management paradigm and suggest that within xeric longleaf pine communities, the primary focus of managed fire regime should be directed toward the restoration of forest floor characteristics rather than the introduction of high-intensity fires used to regulate midstory structure.

**Key words:** duff accumulation; fire; forest floor; litter; longleaf pine; *Pinus palustris*; restoration; sandhill community; structural equation modeling.

### INTRODUCTION

Fire and the genus *Pinus* are inextricably linked over space and time (Agee 1998). Fire not only sustains *Pinus* spp., but is also critical for maintaining the biodiversity of ecosystems dominated by a *Pinus* overstory. Longleaf pine (*Pinus palustris* Miller) woodlands and savannas of the southeastern United States represent an extreme example of a fire dependent ecosystem. These forests have among the shortest fire return intervals of any forest in the world, with fires typically recurring every 1–10 years (Christensen 1981, 1988, Bridges and Orzell 1989, Abrahamson and Hartnett 1990, Chandler et al. 1991, Ware et al. 1993, Glitzenstein et al. 1995). The understory of longleaf communities is extremely diverse both in terms of species richness and endemism (Hardin and White 1989). In the contemporary landscape, longleaf pine ecosystems now occupy only 3–5% of

their historical area (Noss et al. 1995, Jose et al. 2006). Large areas of longleaf were converted to different land uses, but a lack of frequent fires has been one of the most widespread factors driving the decline of remaining intact stands (Landers et al. 1995).

Reducing fire return interval has many effects on forest structure. When fires occur with insufficient frequency in longleaf pine communities, a woody midstory dominated by fire sensitive trees and shrubs rapidly develops (Glitzenstein et al. 1995). The development of this midstory often occurs concurrently with a decline in understory diversity. This has led many to conclude that light intercepted by midstory crowns is the salient feature responsible for this decline (Platt et al. 1988a, b, Platt and Rathburn 1993, Brewer and Platt 1994, Brewer 1995, Gilliam and Platt 1999, Provencher et al. 2001a). This mechanism assumes that the developing midstory competitively excludes understory plant species, primarily through light interception.

A less conspicuous change in forest structure associated with infrequently burned stands is the accumula-

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tion of leaf litter and the development of organic soil horizons, collectively called the forest floor (Varner et al. 2005). Frequently burned longleaf pine savannas lack an organic soil horizon as litter is consumed by fires before it can decompose into humus. When fire is excluded, the low fertility of most longleaf pine sites results in extremely slow leaf litter decomposition rates that allow for a high litter accumulation rate (Hendricks et al. 2002). Because litter can influence the physical, biotic, and resource environment of forests, it may also directly regulate understory forest communities (Sydes and Grimes 1981, Facelli and Pickett 1991).

The relative effects of litter and shading on regulating the diversity and density of understory plant species are poorly understood in longleaf pine systems as well as in many other forests. Reanalysis of data reported by Provencher et al. (2001a–c) showed that the impact of litter accumulation might outweigh that of midstory shading. They found that species richness increased as rapidly as one year following fire, even though the fire killed <20% of midstory stems. Although not discussed as a mechanism of degradation, the fire did consume the accumulated litter (Provencher et al. 2001c). In contrast, felling/girdling and herbicide treatments, which resulted in >90% reduction in midstory stems, had little effect on the understory species richness until those treatments were followed by fire three years later (Provencher et al. 2001c).

Our goal in this paper was to understand the relationships among fire, midstory development, forest floor accumulation, and the understory plant community. Clarifying these relationships has potentially profound impacts on forest management. Sustaining biodiversity requires that managers understand how their efforts will affect the structural and functional features of ecosystems, especially if restoration of a degraded system is the goal (Provencher et al. 2001c). The perception that midstory competition drives understory decline has resulted in many managers burning under relatively severe conditions (Varner et al. 2005). High severity fires are needed to reduce the established broadleaf midstory, especially in stands dominated by larger stature individuals (Glitzenstein et al. 1995), but high severity fires are risky in the contemporary southern landscape, and can cause the unwanted death of overstory longleaf trees (Varner et al. 2005, Williams et al. 2006). If forest floor accumulation, as opposed to competition by the midstory, were the dominant cause of reduced understory vigor and diversity, then frequent, low-intensity fires would suffice in the restoration of understory communities without the inherent risks of high severity fires. Furthermore, frequent fires may eventually reduce midstory canopy density given sufficient time.

The relationship among understory diversity and forest structural elements resulting from low fire frequency may be more complex than have been tested to date across the range of edaphic conditions on which

longleaf pine communities occur. Using data collected from northwestern Florida longleaf pine stands with a range of fire histories, we used structural equation modeling (SEM) to examine the relationships among fire, hardwood cover, and forest floor development on understory diversity. SEM allows the testing of both indirect and direct effects among latent variables, which are multivariate constructs of observed variables. Because no single variable adequately captures complex phenomena such as forest structure or understory vigor, latent variables can be more powerful predictors because they are derived from multiple diverse observations. Furthermore, covariance among the predictor variables that precludes traditional forms of regression analyses is eliminated through the construction of the latent variables. An additional power of SEM is its ability to explicitly test causal models and assign effect sizes to the various hypothetical direct and indirect relationships (Malaeb et al. 2000). We report here tests of whether midstory competition or the accumulation of litter and forest floor development explained observed patterns of understory biodiversity. The goal of this research is to understand the structural features regulating biodiversity associated with managed fire regimes. Determining the relative importance of putative causal mechanisms driving understory diversity is important to prescribed fire management, restoration strategies, and setting desired future conditions.

## METHODS

This study was conducted at Eglin Air Force Base during 2002–2003. Eglin Air Force Base, the former Choctawhatchee National Forest, is located on the panhandle of Florida, USA, and serves as an important reservoir for the longleaf pine ecosystem, containing nearly  $18 \times 10^4$  ha of longleaf pine and over half of the remaining old growth (Varner et al. 2000, Holliday 2001). All study sites were within the Southern Pine Hills District of the Coastal Plain Physiographic Province with deep, well-drained sandy soils (Brown et al. 1990). Soils of the study sites were all typic Quartzipsamments of the Lakeland series with mean depth to water table >200 cm (Overing et al. 1995). The climate of the area is subtropical, with warm, humid summers and mild winters. Mean annual temperatures in the area are 19.7°C, with a mean annual precipitation of 1580 mm, most of which falls from June to September (Overing et al. 1995). Elevations of the study sites were 52–85 m above sea level, and all sites had the minimal topography typical of sandhills (Myers 1990). Vegetation was dominated by a longleaf pine overstory with a midstory of various deciduous oaks, e.g., *Quercus laevis* Walter, *Q. margaretta* Ashe, *Q. incana* Bartram, *Q. germinata* Small. Low fire frequency has led to the increase in density and crown cover of deciduous oaks as well as the expansion of *Pinus clausa* Vasey into the ecosystem and an increased presence of evergreen oaks such as *Q. virginiana* Miller (McCay 2000).

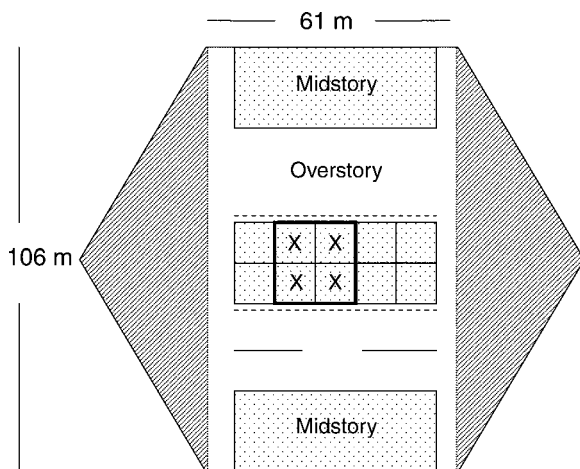


FIG. 1. Schematic of vegetation sampling plots. Overstory variables were measured in the  $61 \times 106$  m plot nested within the 1-ha monitoring area. Midstory stems were sampled in the three  $10 \times 50$  m subplots. Understory was measured in the four  $10 \times 10$  m squares marked with an X. Duff and litter were measured along the dashed lines above and below the middle midstory subplot. Species richness was calculated in the four  $10 \times 10$  m modules marked with an X ( $400 \text{ m}^2$ ). Density of different species and guilds was determined from eight 1-m subplots within each of the species richness modules.

Eglin Air Force Base established a long-term monitoring program in 2001 to determine the effects of disturbance and management on plant communities. We analyzed a subset of these data in the results reported here. The monitoring is based on 1-ha plots (200 as of 2003) randomly located across the base. Within each plot, overstory measurements were taken in a rectangle ( $61 \times 106$  m) running north to south (Fig. 1). Within this area, the height and diameter of all trees  $>10$  cm diameter at 1.37 m (diameter at breast height, dbh) were measured. Midstory measurements were taken in three  $50 \times 20$  m subplots nested within the overstory measurement plot (Fig. 1). Within these midstory plots, all trees with a dbh  $<10$  cm were tallied by species and diameter class.

Understory measurements were taken in four  $10 \times 10$  m modules within the middle midstory subplot (Fig. 1). Species richness (total number of species per  $400 \text{ m}^2$ ) was tallied within the four modules. The density of grasses and legumes was recorded in two  $1\text{-m}^2$  plots per  $10 \times 10$  m module. Consequently, eight subsamples were used to calculate the understory density of each species. Other understory response variables used in this study were: (1) stem density for all species with the bunchgrass growth form including some species within the genera *Andropogon*, *Schizachyrium*, *Aristida*, *Sporobolus*, *Sorghastrum*, and *Panicum*, (2) stem density for all non-bunchgrass species in the genera *Andropogon* and *Schizachyrium*, and (3) stem density for all species in the family Fabaceae. Members of each understory category were chosen based on similarity of life history traits. The more inclusive bunchgrass guild was chosen

because these species collectively allow for frequent fire. Bunchgrasses are an important component of the fuel bed because they burn readily, perch fallen pine needles on grass litter, and quickly resprout following fire. For all analyses, the understory response variables were cube-root transformed to linearize the relationships and equalize the residuals. Along a 100-m point-intercept transect across the top and bottom of the middle midstory subplot, the depth of leaf litter ( $O_i$  horizon) was measured every 10 m and averaged for each plot (Fig. 1). Litter constituted surface materials that retained their original form ( $O_i$  horizon). Duff ( $O_e$  and  $O_a$  horizon) constituted organic materials beneath the litter layer that were fermented and decomposed. Duff accumulation can be highly variable across space, but builds more rapidly in the absence of fire around the base of canopy longleaf pine. Thus, to gain a more sensitive measure of forest floor development under inadequate fire regime, duff was measured to the nearest 0.1 cm at the base of each canopy longleaf within the overstory sampling areas (Fig. 1). All duff data were averaged across trees to generate one value per plot, thus making the measurement of duff accumulation an index of forest floor development at the plot scale. Fire frequency over the last 30 years was determined from historical records. Appendix A contains a complete description of variables, abbreviations, and their units used in this study.

During June–September 2003, hemispherical photographs were taken at the center of the hexagon with a Nikon CoolPix 990 digital camera with a fisheye lens adaptor at a height of  $\sim 1$  m in a subset of 69 plots. Photos were taken when the sun was behind clouds or below the horizon, i.e., dusk or dawn, to standardize image quality and prevent errors due to reflections. Photos were analyzed using WinSCANOPY Version 2004 (Regent Instruments, Quebec City, Canada) to determine the percentage openness of the canopy, i.e., the amount of sky unobstructed by vegetation. The estimate of openness provided by WinSCANOPY takes into account the relative spherical area occupied in elevation rings. Before calculating openness, each photo was adjusted to allow for the greatest contrast between the canopy and the sky. Canopy openness derived from hemispherical photographs provides an accurate and unbiased estimate of within growing-season light availability in these pine-woodland systems (Battaglia et al. 2003). When compared in a subset of 16 plots, the estimates of canopy openness from the hemispherical photographs were highly correlated with direct ceptometer measurements of photosynthetically active radiation transmitted to the forest floor ( $r^2 = 0.85$ ).

#### Statistical analysis

We used the software AMOS version 5.0.1 (Small Waters, Chicago, Illinois, USA) to perform SEM on the relationships among the direct and indirect effects of fire, canopy cover, and forest floor on understory plant

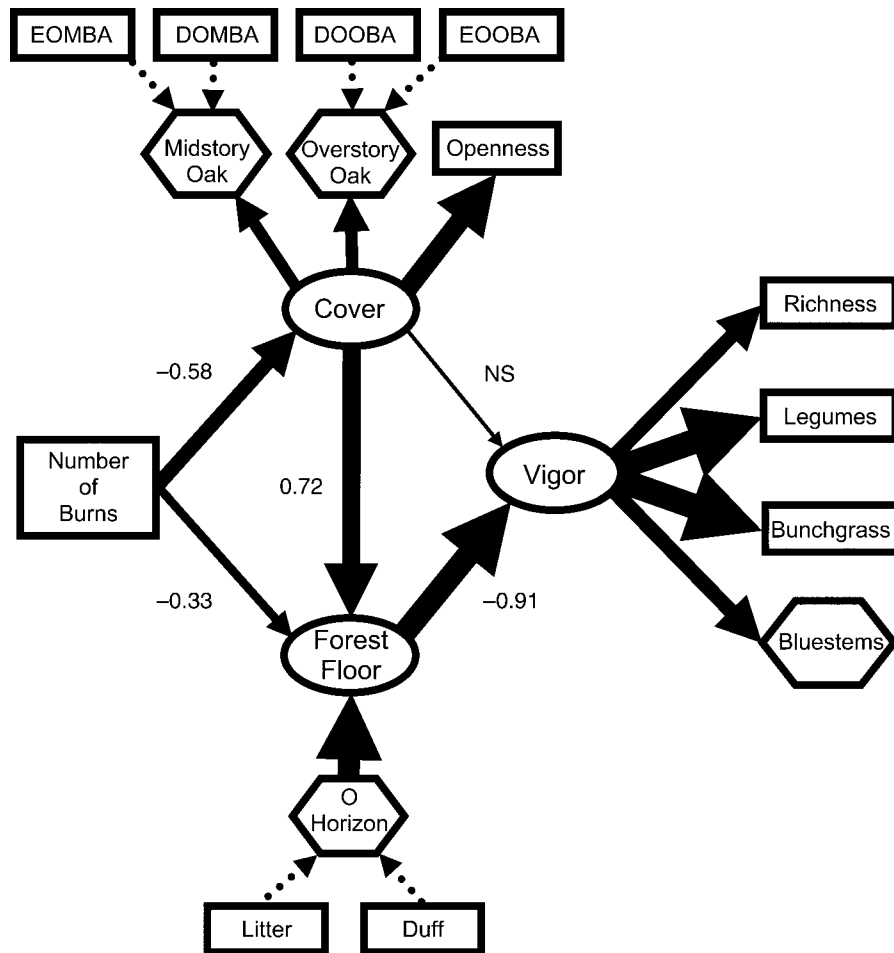


FIG. 2. Path diagram of the structural equation modeling (SEM). The shapes and arrows in the diagram indicate the type of variable and their relationships; rectangles show indicator variables or direct observations, hexagons are composite variables created by combining the direct observations indicated by the dotted arrows, and ellipses are latent variables. Solid arrows represent both putative causal relationships among latent variables and their relationship with observed variables, with the arrow thickness determined by the strength of the correlation. The values next to the solid arrows among the core of the model are standardized regression coefficients. All correlations were significant at  $\alpha = 0.05$  with the exception of the direct effect of cover on diversity. Variable descriptions are found in Appendix A, and detailed SEM results are in Appendix B.

diversity. Fig. 2 shows both the structure and the results of the model we tested. The construction of the SEM was based on our conceptual model of the direct and indirect effects of midstory cover and forest floor on indicators of understory vigor. The model included seven observed, three composite, and three latent variables (Fig. 2). The dependent latent variable, vigor, was derived from the observed variables of understory species richness, legume density, bluestem density, and bunchgrass density as described previously. The independent latent variable, cover, was derived from canopy openness and two composite variables, each being the respective sums of oak basal area in the overstory and midstory. The latent variable, forest floor, was derived from a composite variable that consisted of the sum of the litter and duff layer depths at the plot scale. We chose to create the composite variables because they represented stand characteristics we specifically wanted

to test and simplified the model (see Harrison et al. 2006).

Following the SEM analysis, we performed boundary line regressions (Webb 1972, Schmidt et al. 2000) with elements of understory diversity as dependent variables and using duff depth as the predictor. Duff was chosen as the predictor because it explained more variation than canopy cover in all the understory responses, but these data were collected at the stand scale, and thus duff serves as an index of forest floor development. For each understory response, the data from the 69 plots were arranged in order from least to greatest duff depth. The data were then broken into groups of seven pairs with the last group having only six pairs. For each group, the pair with the highest value for the response variable was selected, giving a total of 10 pairs. A curve was then fit to these pairs of data to represent the maximum expected understory response for a given duff depth.

## RESULTS

*Stand characteristics*

As expected with a history of variable fire frequency, the xeric longleaf pine sandhills in this study represented a full range of site conditions, especially with respect to midstory encroachment. Midstory characteristics in this study averaged 1016 hardwood stems/ha, ranging from 0 to 5019 stems/ha. Midstory hardwood basal area (BA) averaged 6.14 m<sup>2</sup>/ha, ranging from 0 to 29.93 m<sup>2</sup>/ha. Canopy hardwoods contributed additional BA ranging from 0 to 17.75 m<sup>2</sup>/ha, averaging 4.05 m<sup>2</sup>/ha across all plots. Together across all strata, total hardwood BA ranged from 0 to 38.01 m<sup>2</sup>/ha, averaging 10.08 m<sup>2</sup>/ha. Analysis of hemispherical photographs showed that total openness ranged from 9.9% to 81.6%, with a mean of 42.9% openness across all plots.

Understory species richness also varied considerably among plots, ranging from 26 to 106 species/400 m<sup>2</sup>, with an average of 61 species/400 m<sup>2</sup> across all plots. Forest floor accumulation ranged from 0.19 to 14.83 cm, averaging 4.68 cm/plot. A detailed table of forest stand and dependent variable summary statistics can be found in Appendix B.

*Structural equation model*

The SEM developed for this study fit the data well as determined by a suite of goodness-of-fit indices recommended by Kline (1998) and Hu and Bentler (1999). These and the complete results of the analysis can be found in Appendix C. For the general model, all the standardized regression coefficients were significant ( $P < 0.05$ ) for all relationships except the direct effect of cover on vigor. The magnitudes of the direct and indirect relationships among the latent variables are shown in Fig. 2. All relationships among observed and composite variables and their corresponding latent variables were significant. Cover was positively correlated with the observed variables midstory and overstory oak basal area but was negatively correlated with openness. Vigor was positively correlated with all associated observed variables. Forest floor was positively correlated with the composite variable O horizon. The latent variables, cover and forest floor, were positively correlated with each other and negatively correlated to number of burns. Vigor was, however, not directly correlated to cover, but was directly negatively correlated with forest floor. Detailed tables of regression coefficients and squared multiple correlations can be found in Appendix C.

The results of the SEM analysis indicate that midstory encroachment represented as cover has no direct influence on understory characteristics tested in this model (Fig. 2). While cover had no significant direct effect on vigor, the accumulation of the forest floor was significantly and positively correlated with cover, indicating an indirect negative effect of midstory cover on understory vigor mediated through forest floor

development. The model confirmed that frequent fires decreased both cover and forest floor.

*Boundary line analysis*

The boundary line analyses (Fig. 3) were all significant at  $\alpha = 0.05$  and indicated a negative linear relationship ( $r^2 = 0.34$ ) between duff depth ( $\delta$ ) and species richness represented by the following equation: species richness =  $4.52 \times \delta + 87.3$ . The analysis also showed negative curvilinear relationships among  $\delta$  and measures of understory density as shown by the following equations: bluestem =  $19.01 \times e^{(-2.05\delta)}$ , bunchgrass =  $37.9 \times e^{(-0.63\delta)}$ , legumes =  $22.9 \times e^{(-0.32\delta)}$ , and *Schizachyrium* =  $-3.92 \times \ln \delta + 9.94$ . The variances explained by the equations were 0.64, 0.66, 0.66, and 0.90 for bluestem, *Schizachyrium*, legume, and bunchgrass density, respectively. Because measurement of duff accumulation in this study is at the plot scale, it represents an index of forest floor development. The curvilinear relationship between understory density and duff depth demonstrates a high sensitivity of understory plants to small amounts of forest floor development and subtle changes in fuel bed characteristics. For instance, within a stand that averages a duff depth of 2 cm (maximum depth 8.8 cm) at the base of longleaf pine trees, there is a potential maximum decline of 60%, 75%, 45%, and 70% in bluestem, *Schizachyrium*, legume, and bunchgrass density, respectively, within the plots. The densities of all species within the plots approached zero at ~5–6 cm of duff at the base of trees within the stand. In contrast, the maximum expected species richness decreased from ~90 to 50 species/400 m<sup>2</sup> across the range of measured duff depth.

## DISCUSSION

The results of the structural equation model showed forest floor development to be the likely causal mechanism by which fire suppression and the presence of midstory hardwoods affect species richness and understory guilds in xeric longleaf sandhills. Light attenuation by oaks was not seemingly a direct cause of degradation on understory vigor, rather oak effects were mediated through the contribution of litter to forest floor development. It appears that in this study, hardwoods light interception did not exceed thresholds of light attenuation needed to suppress understory vigor even at relatively high densities of sandhill hardwoods. The relative openness of the plots in this study (42.9% openness on average) falls within the range of values reported by Battaglia et al. (2003) for second growth, frequently burned longleaf pine woodlands.

While previous studies have established a link between understory communities and light environment (e.g., Riegel et al. 1995, Hains et al. 1999, Naumburg and DeWald 1999) and litter accumulation (e.g., Sydes and Grime 1981, Peterson and Facelli 1992, Facelli et al. 1999), very few have attempted to analyze these two related factors together. A study examining the response

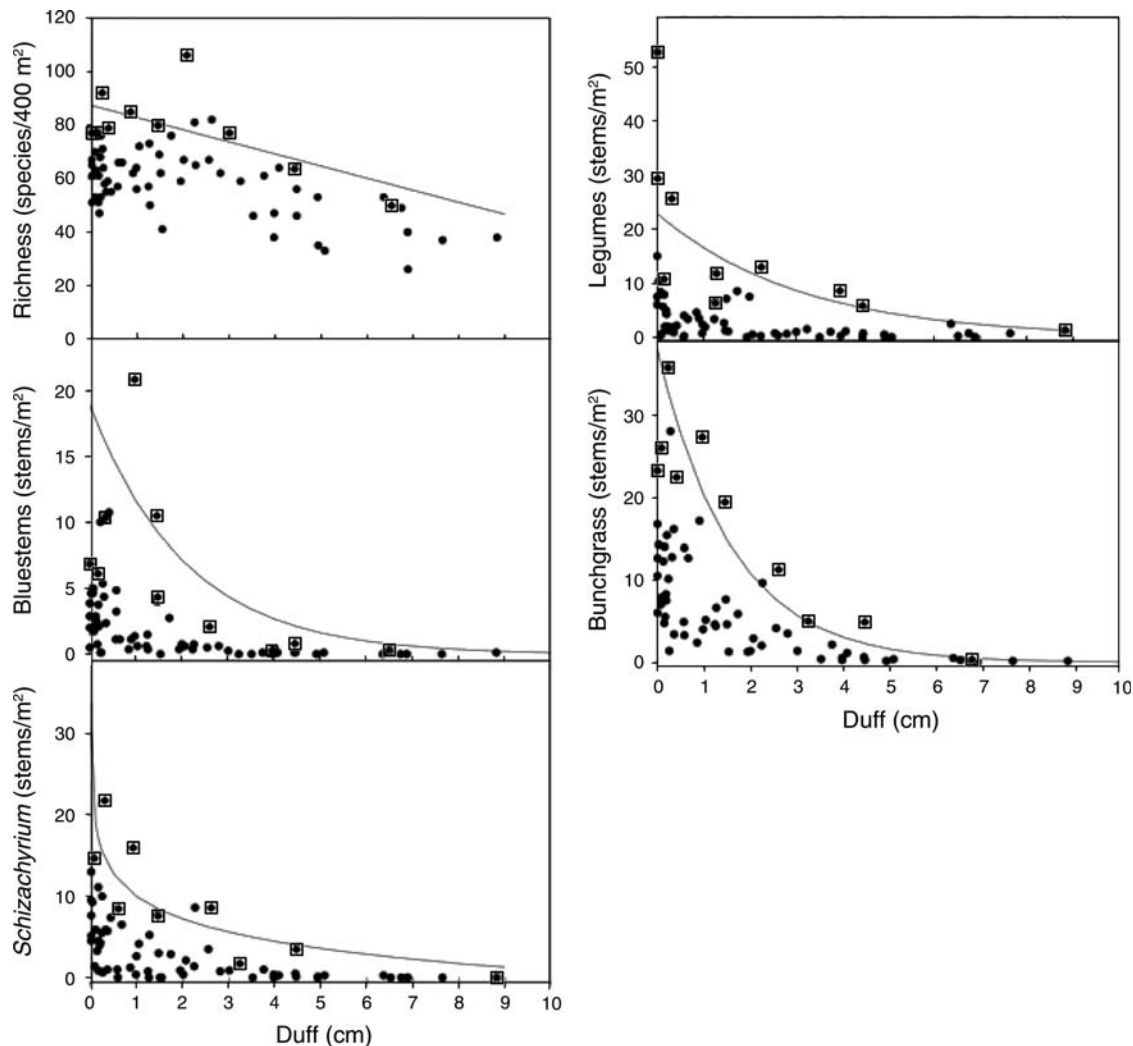


FIG. 3. Boundary-line analysis between response variables and duff depth. A solid line represents maximum expected response to increasing duff depth based on curves fit to points surrounded by open squares.

of understory vegetation beneath closed canopy longleaf pine plantations in South Carolina found that light interception from dense canopies had a larger negative effect on planted understory seedlings than pine litter (Harrington and Edwards 1999, Harrington et al. 2003). While the results of Harrington et al. are informative and offer insight into using containerized seedlings for restoration, caution must be exercised when applying their results to non-plantation settings or in xeric, open stands that contain significant oak litter and naturally occurring populations of understory plants.

An example of the inconspicuous nature of the effects of forest floor on the understory plant community can be found in a long-term study conducted to compare the effects of fire and fire surrogates for removing midstory oaks (Provencher et al. 2001a, b). While mechanical felling, girdling, and herbicides dramatically decreased midstory oak density when compared to spring burning, only burning had a significant positive effect on

understory density and species richness. Those results are similar to our finding that forest floor development has a greater negative impact than direct competition for light on understory communities in fire suppressed, xeric sand hill ecosystems.

Litter has been reported to represent a physical barrier to plant growth and impede community development, and this mechanism may explain the negative impact of the forest floor on understory communities in longleaf ecosystems. In deciduous woodlands, the ability of sprouting understory species to penetrate the litter layer was related to morphology (Sydes and Grimes 1981). Species whose leaves grew vertically before unfolding were moderately successful in penetrating the litter layer while those that grow from a basal meristem, such as grasses, were not able to penetrate the litter. The longleaf pine ecosystem is dominated by grasses and species that resprout after fire from a basal meristem. Historically, frequent fires consumed most

leaf litter; therefore, understory species vigor might be particularly sensitive to litter accumulation.

In addition to litter acting as a physical barrier, the forest floor might negatively influence understory plants through phytotoxins, light interception, temperature changes, or altered water status (Facelli and Pickett 1991). Litter leachates have been shown to inhibit germination (Facelli and Pickett 1991); however, most studies have been conducted in the laboratory and their relevance to plant community dynamics is not yet established. Nevertheless, oak litter is rich in tannins and other chemical compounds that may influence understory plants via altered nutrition, or allelopathy. Litter also inhibits understory plants by producing shade at the soil surface and some seeds need light to break dormancy (Vazquez-Yanes et al. 1990). Likewise, species with little energy stored in the seed need to photosynthesize immediately upon germination to survive. If inadequate light is available, they will suffer carbon stress, reducing vigor and possibly causing mortality (Willms 1988). Most of the understory species in the longleaf pine ecosystem we measured were perennial and resprout after fire. Therefore, interference of germination by the litter may not drive patterns of degradation in the short term, but could inhibit recovery of the system over longer periods of fire exclusion. More importantly, shade at the surface alters the allocation of carbon among leaves and roots within adult clonal plants with fewer ramets being produced (Evans 1991, 1992).

The curvilinear boundary line response of understory species showed a threshold sensitivity of the understory to the development of an organic soil horizon within the stand. Because our duff measurements were taken at the base of trees within plots to increase the sensitivity of our observations, these data represent an index of forest floor development at the stand scale and likely integrate subtle but important changes in the fuel bed that are responsible for declines in biodiversity. Consequently, burning xeric sites as frequently as fuels allow preventing forest floor development would be important for maintaining high densities of understory species, regardless of midstory stem density. A long-term study that examined community responses to annual, biennial, and quadrennial fire return intervals in mesic longleaf pine stands in South Carolina and northeast Florida found that annual burning resulted in the highest cover and richness of nonwoody understory plants (Glitzenstein et al. 2003). We found a linear boundary line response of species richness to duff depth at the stand scale. This could indicate that while species densities quickly decline with forest floor development, overall species richness may be more resilient to periods of fire exclusion. This was consistent with the patterns of recovery reported by Provencher et al. (2001c), which showed a rapid recovery of understory species after just one prescribed burn.

Although our data showed that forest floor accumulation and light environment were two of the dominant mechanisms affecting most understory species responses, the high variation in understory response for a given duff depth in the boundary line analyses indicated that other unexplored factors were also important. Some factors may be related to environmental constraints we did not measure such as soil texture, depth to water table, or intensity of belowground competition. In addition, much of the unaccounted variation across the expansive study area could have been related to variation in previous land use history, proximity to seed sources, or other dispersal limitations. Examining the responses of groups of species with similar life histories helped eliminate many of these stochastic factors that could have affected the presence or absence of individual taxa.

It is important to note that while direct competition and competitive exclusion by shading from the canopy was not the primary force driving understory degradation on xeric longleaf pine sandhills, these results do not suggest that midstory encroachment cannot achieve canopy closure sufficient to eliminate groundcover diversity elsewhere. Xeric sites represent an extreme case; even with stem densities as high as 2000–3000 stems/ha, Provencher et al. (2001c) found canopy closure values of no more than 60%. On more mesic sites with greater leaf area and light interception, direct competition through shading could be the primary source of midstory decline as has been often reported in the literature, though no previous studies included an examination of the impact of forest floor (Platt et al. 1988a, b, Platt and Rathburn 1993, Brewer and Platt 1994, Brewer 1995). It is possible that rather than representing one end of a gradient, xeric longleaf sandhills might differ in kind rather than degree from mesic longleaf pine communities with respect to the influence of midstory encroachment on patterns of degradation and restoration.

From a management perspective, fire frequency is the most important factor related to understory species density and diversity and has been reported elsewhere (Brockway and Lewis 1997, Glitzenstein et al. 2003). Consistent with Glitzenstein et al. (2003), our results support their conclusion that to maintain a healthy understory, fires should occur as frequently as fuels allow. The shift in focus away from oak elimination offers managers greater flexibility when applying prescribed fire, due to the fact that fires capable of eliminating midstory oak encroachment after decades of insufficient fire often require burning under extreme conditions or marginal prescription windows. Moreover, fuel build-up is often used to achieve greater fire intensity by lengthening fire return intervals, which our results indicate would exacerbate understory decline. In addition to narrowing the prescription window for fire management, such burns are more likely to escape or cause extensive longleaf overstory mortality (Williams et

al. 2006), particularly when duff is present (Varner et al. 2000, 2005). If maximizing understory diversity is a manager's goal, our results suggest that the link between forest floor development and biodiversity should be of primary concern. Managers should refine their application of fire and fire surrogates to focus on forest floor reduction rather than opening the midstory canopy in xeric longleaf stands.

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## APPENDIX A

A table explaining the abbreviations and units of measurement for all variables described in the text (*Ecological Archives* A017-031-A1).

## APPENDIX B

A table of summary statistics of forest structure and understory variables measured (*Ecological Archives* A017-031-A2).

## APPENDIX C

Tables of detailed results of the structural equation model including fit statistics and tables of regression coefficients and squared multiple correlations for variables included in the model (*Ecological Archives* A017-031-A3).